Systematics evolution and distribution of mussels belonging to the genus *Mytilus*: an overview

Raymond Seed

School of Ocean Sciences, University of Wales-Bangor, Menai Bridge, Gwynedd, LL59 5EY, United Kingdom

Abstract. Despite their scientific and commercial interest and their widespread distribution throughout the cooler waters of both northern and southern hemispheres, the taxonomy of mussels belonging to the genus *Mytilus* remains controversial. This paper reviews the systematics of this group, albeit with particular emphasis on the smooth-shelled mussels of the *M. edulis* complex, and stresses throughout the need for a multidisciplinary approach. Multivariate analysis of allozyme and morphometric data obtained for mussels worldwide now provides compelling evidence for the existence of three distinct evolutionary lineages: *M. edulis; M. galloprovincialis; M. trossulus.* No single taxonomic character discriminates unequivocally among these taxa though certain characters, either individually or in combination, are virtually diagnostic. All three lineages occur in northern waters but only *M. edulis* and *M. galloprovincialis* have so far been recorded from the southern hemisphere. Whether these taxa are accorded full specific status will require an agreed operational definition of biological species. Future research should focus on the biological mechanisms that maintain the distinctive characteristics of these mussels across vast distances despite the occurrence of hybridisation and the massive potential for larval dispersal. The origin, evolution and distribution of mussels within the genus are discussed.

The genus *Mytilus* is one of the most cosmopolitan of all marine genera, occurring at higher latitudes in all oceans and major seas of both northern and southern hemispheres. It is found intertidally and subtidally, in estuarine and fully saline habitats, attached by means of byssal threads to a wide variety of hard or semiconsolidated substrata. In view of its widespread distribution, as well as its scientific and commercial importance, it is perhaps surprising that the taxonomy and systematics of this extensively studied genus still remains a somewhat controversial issue (e.g. Gosling, 1984; McDonald *et al.*, 1991).

Much of the early taxonomy of *Mytilus* was based solely on morphological features, particularly those pertaining to the shell. However, ontogenetic and environmentally induced variation in shell characteristics (e.g. Seed, 1968, 1973, 1978; Lewis and Seed, 1969), combined with the complex interactions that are now known to exist among several taxa within this genus, has produced an extremely confused and largely erroneous taxonomy (Koehn, 1991). In a comprehensive review of the genus, Lamy (1936) recognised the following smooth-shelled mussels as distinct species: *M. edulis* Linnaeus from north temperate waters; *M. galloprovincialis* Lamarck from the Mediterranean Sea; *M. trossulus* Gould from the Pacific coast of North America, *M. chilensis* Hupé and *M. platensis* Orbigny from the east and west coasts of South America respectively; *M. planulatus* Lamarck from Australia and New Zealand. He also described *M. desolationis* Lamy (= *M. kerguelensis* Fletcher) from the Kerguelen islands in the southern Indian Ocean. These taxa, however, were reported by Soot Ryen (1955) as geographical subspecies or races of the *M. edulis* species complex. Other taxa previously considered to be subspecies of *M. edulis* include the Californian bay mussel, *M. diegensis* Coe (Soot Ryen, 1955) and *M. aoteanus* Powell from New Zealand (Fleming, 1959) together with *M. kussakini* and *M. zhirmunskii* from the Pacific coast of Asia (Scarlato and Starobogatov, 1979).

Mytilus californianus Conrad, a distinctively different species of large body size and divergent ecology to *M. edulis*, is identified readily by the presence of radiating ribs on the shell (Soot Ryen, 1955). *M. coruscus* Gould (= *M. crassitesta* Lischke) is a thick-shelled, ribbed mussel with minute crenulations along the ventral margin close to the apex (Kira, 1962). Unfortunately, however, we have little or no detailed information regarding this mussel and its systematic status thus remains uncertain. Recently, Vermeij (1989) has speculated that *M. californianus* and *M. coruscus* could in fact comprise a single species with geographical variations in the prominence of the radiating ribs. However, because both of these mussels are distinguished easily from the smooth-shelled mussels of the *M. edulis* group, they will not be considered in any detail in this paper.

The use of enzyme electrophoresis to characterise individual and population differences in genetic composition, together with multivariate techniques applied to both enzyme and morphometric phenotypes, have assisted greatly in elucidating the systematics and taxonomic status of species of smooth-shelled mussels (e.g. McDonald and Koehn, 1988; Varvio *et al.*, 1988; McDonald *et al.*, 1991). Although three

taxa have been identified *(Mytilus edulis, M. galloprovincialis* and *M. trossulus)*, hybridisation has been reported at most locations where the ranges of these mussels coincide and consequently this has led to considerable speculation regarding their taxonomic status (e.g. Skibinski *et al.*, 1983; Gosling, 1984, 1992; McDonald and Koehn, 1988; Johannesson *et al.*, 1990; Väinölä and Hvilsom, 1991). In this paper I shall document briefly the evidence for the existence and distribution of these three relatively distinct mussels, albeit with particular emphasis on the taxonomic validity of the Mediterranean mussel *M. galloprovincialis*, which was originally thought to be restricted to European coasts but which now appears to be far more widely distributed (e.g. Wilkins *et al.*, 1983; Lee and Morton, 1985; Grant and Cherry, 1985; McDonald and Koehn, 1988; McDonald *et al.*, 1991). Much less information is available currently concerning the systematics, distribution and ecological characteristics of *M. trossulus*.

SYSTEMATIC CHARACTERISATION OF *MYTILUS*

A) ENZYME ELECTROPHORESIS: Allozyme characters have assisted greatly in clarifying the complex biosystematics of the genus *Mytilus*. Despite the large number of enzymes that are potentialy available for study, in practice only a few have sufficiently high levels of variation to be of significant taxonomic value (e.g. Ahmad *et al.*, 1977). Earlier studies on the *M. galloprovincialis-M. edulis* complex (reviewed by Gosling, 1984) used various combinations of six loci; esterase D *(Est-D)*, leucine aminopeptidase *(Lap-1)*, glucose phosphate isomerase *(Gpi)*, aminopeptidase *(Ap)*, peptidase 2 *(Lap-2)* and phosphoglucomutase *(Pgm)*. More recently, octopine dehydrogenase *(Odh)* and mannose phosphate isomerase *(Mpi)* have also been incorporated into the suite of enzymes used to differentiate between these smooth-shelled mussels (e.g. Skibinski, 1983; Grant and Cherry, 1985; Varvio *et al.*, 1988; McDonald and Koehn, 1988). None of these loci, however, discriminate unequivocally between *M. edulis* and *M. galloprovincialis*, but according to Varvio *et al.* (1988) the *Mpi* locus is 'virtually diagnostic'. McDonald and Koehn (1988) similarly found that *Mpi* was diagnostic in almost all the allopatric populations of *Mytilus* that they studied although a combination of other loci with large differences in allele frequency could also effectively discriminate between different taxa. When a combination of four allozyme loci were used, Sanjuan *et al.* (1990) found that the probability of misclassification was exceedingly low (1.5×10^{-7}); indeed 99% of all individual mussels in their samples could be assigned correctly on the *Est-D* genotype alone. Although a less well studied enzyme, leucyl glycyl glycine peptidase is also reported to provide an almost perfect discrimination between *M. edulis* and *M. galloprovincialis* (Grant and Cherry, 1985). The principal loci used in studies of *Mytilus* genetics, especially those which have proved to be most valuable in taxonomic studies, are comprehensively reviewed by Gosling (1992).

Beaumont *et al.* (1989) examined allele frequencies at three loci *(Est-D, Mpi, Odh)* in mixed populations of *Mytilus edulis* and *M. galloprovincialis* from two physically contrasted sites, Rock and Polzeath, in the Camel estuary in south-west England, and a pure population of *M. galloprovincialis* from Langebaan lagoon on the west Cape coast of South Africa. Their results, summarised in Table 1, reveal markedly different allele frequencies between these two mussels, particularly with respect to the *Est-D* and *Mpi* loci. At Rock, the *Mpi* locus proved to be less effective at differentiating *M. edulis* and *M. galloprovincialis* than the *Est-D* locus, whilst both of these loci were rather poor discriminators in the South African and Polzeath populations. *Odh* genotypes did not appear to be particularly good discriminating characters in any of the populations studied though the data of Varvio *et al.* (1988) did allow clear discrimination of *M. galloprovincialis* populations on the basis of *Odh* allelic composition. A further feature of the Rock mussel population was the disparity in the percentage of *M. edulis* compared to *M. galloprovincialis* that were misidentified by the *Mpi* locus. This is owing to the fact that the Mpi^{63} allele (the characteristic *M. galloprovincialis* allele) was present in the *M. edulis* population at a frequency of 0.197 but the reverse was not true as the *M. edulis* allele, Mpi^{100}, was present in the *M. galloprovincialis* population at a frequency of only 0.053 (Table 1).

Two salient features would thus appear to emerge from the use of single locus genotypes as characters for discriminating between *Mytilus edulis* and *M. galloprovincialis*. Firstly, a locus can give good discrimination in one

Table 1. Allele frequencies at three loci in sympatric populations of *Mytilus edulis* and *M. galloprovincialis* from Rock and *M. galloprovincialis* from Polzeath and South Africa (after Beaumont *et al.*, 1989).

Locus	Alleles (relative mobility)	Allele frequencies Rock *M. edulis*	Rock *M. gall.*	S. Africa *M. gall.*	Polzeath *M. gall.*
Esterase-D	60	0.014	—	—	—
(Est-D)	82	0.021	0.941	0.802	0.360
	100	0.936	0.059	0.198	0.640
	118	0.029	—	—	—
Mannose	63	0.197	0.947	0.882	0.722
phosphate	100	0.796	0.053	0.118	0.278
isomerase	133	0.007	—	—	—
(Mpi)					
Octopine	60	0.007	0.006	—	0.015
dehydro-	70	0.111	0.530	0.540	0.634
genase	77	0.014	—	0.030	—
(Odh)	100	0.799	0.226	0.120	0.227
	106	0.014	0.006	—	0.015
	112	0.055	0.232	0.310	0.109

population but poorer discrimination in another, and, secondly, a locus may be diagnostic for one species, but not the other, within any single mussel population (Beaumont *et al.*, 1989). Variations in genotype, whether on a local or geographical scale, could of course reflect differential patterns of environmental selection rather than distinct evolutionary backgrounds (e.g. Murdock *et al.*, 1975; Koehn *et al.*, 1980; Gartner-Kepkay *et al.*, 1983; Johannesson *et al.*, 1990; Tedengren *et al.*, 1990). The marked differences in allele frequencies reported for the mussel populations at Rock, however, cannot easily be attributed to such causes since these mussels occur within mixed clumps and are thus presumably subjected to identical environmental conditions.

On the basis of five allozyme loci, Koehn *et al.* (1984) were able to separate samples of putative *Mytilus edulis* from several sites throughout eastern North America into three distinguishable groups, though one of these involved separation at a single locus *(Lap)* and was not, therefore, thought to represent a distinct taxonomic group. The other two groups, however, were very different at several loci and this led these authors to suggest that one of these groups represented a hitherto unrecognised species. Subsequently, this was given additional support by Varvio *et al.* (1988) who showed that this mussel was most similar to *Mytilus* from the Baltic Sea (see also Bulheim and Gosling, 1988) and which is now recognised as *M. trossulus*, a species reported previously only from parts of the Pacific coast of North America (e.g. McDonald and Koehn, 1988).

More recently McDonald *et al.* (1991) used a multivariate technique to analyse the electrophoretic data at eight loci in over a thousand mussels collected from a total of 45 sites in the northern and southern hemispheres. Allozyme data (71 characters) were reduced and displayed using principal component analysis which locates the orthogonal axes accounting for the greatest amount of variation in the multidimensional space. This analysis defined three distinct clusters of individuals in the northern hemisphere samples but only two clusters in southern hemisphere mussels, albeit with some intermediate individuals mainly from those sites where these mussels come into contact and hybridisation occurs (Figs. 1A,B). Each cluster in the northern hemisphere could be assigned to an extant species, *Mytilus edulis, M. galloprovincialis* or *M. trossulus*, based on the examination of principal component scores of individuals from locations where the identity of mussels had been designated previously (e.g. McDonald and Koehn, 1988; McDonald *et al.*, 1990).

The *Mytilus edulis* cluster in the southern hemisphere, comprising mussels from South America, the Falklands and Kerguelen islands (= "South American mussels"), were most similar to northern hemisphere *M. edulis*, although they did contain alleles that were characteristic of all three northern mussels. The reason for this is that many loci of these "South American" mussels contained alleles that in northern hemisphere mussels were common only in *M. galloprovincialis* or *M. trossulus*. Blot *et al.* (1988) has similarly shown that mussels from the Kerguelen islands were more similar genetically to northern *M. edulis* than to *M. galloprovincialis*. Mussels from Australia, Tasmania and New Zealand (= "Australian mussels") formed the second southern hemisphere cluster with principal component scores similar to *M. galloprovincialis* from the northern hemisphere, though once again there were some differences in allele frequencies, particularly at the *Mpi* and *Est-D* loci. Mussels from South Africa have similar allelic frequencies to *M. galloprovincialis* from the Mediterranean Sea and south-west England (Grant and Cherry, 1985; Beaumont *et al.*, 1989; Table 1).

B) MORPHOMETRIC CRITERIA: Overall shell morphology in *Mytilus* is subject to considerable phenotypic variation. Such environmental control of shape (and growth rate) is readily demonstrated by transplanting mussels from one habitat to another and recording the resulting changes in morphology [see Seed and Richardson (1990) and references therein]. Moreover, such environmentally induced variations are further confounded by ontogenetic changes in shape brought about by allometric growth (Seed, 1968, 1973, 1978, 1980). Similar trends are exhibited by both *Mytilus edulis* and *M. galloprovincialis* resulting in a considerable degree of convergence so that, in some populations, shell characters merge until identification on gross morphology alone becomes difficult or impossible. Intermixing of morphological characters in sympatric populations could also be due to hybridisation between these two mussels (e.g. Seed, 1972, 1974). In some populations, however, differences in gross shell morphology between *M. edulis* and *M. galloprovincialis* can be extremely pronounced. At Rock, for instance, where these two mussels occur in mixed populations, *M. galloprovincialis* has a significantly taller shell with a steeper ligamentary angle (the angle subtended by the ventral and ligamentary margins, see Fig. 2A) than *M. edulis*. Maximum shell width lies closer to the ventral margin and consequently the ventral aspect of *M. galloprovincialis* is much flatter when viewed in cross section (Figs. 2B, C). Typically *M. galloprovincialis* has a more pointed, beaked or ventrally incurved shell with a rather triangular shaped outline whereas *M. edulis* is more rounded anteriorly, has a more elongate, cylindrical shell with a straight or even slightly convex ventral margin. Thus, at Rock, several shell features combine within single individuals to produce mussels which are quite distinctive in their overall external appearance (Figs. 3H, I). Furthermore, these different morphologies are maintained amongst all size ranges of mussels strongly suggesting that they are, in fact, genetically rather than environmentally controlled (Beaumont *et al.*, 1989; Seed, 1990). Many of these features also recur in mussels from different parts of their geographical range (Figs.

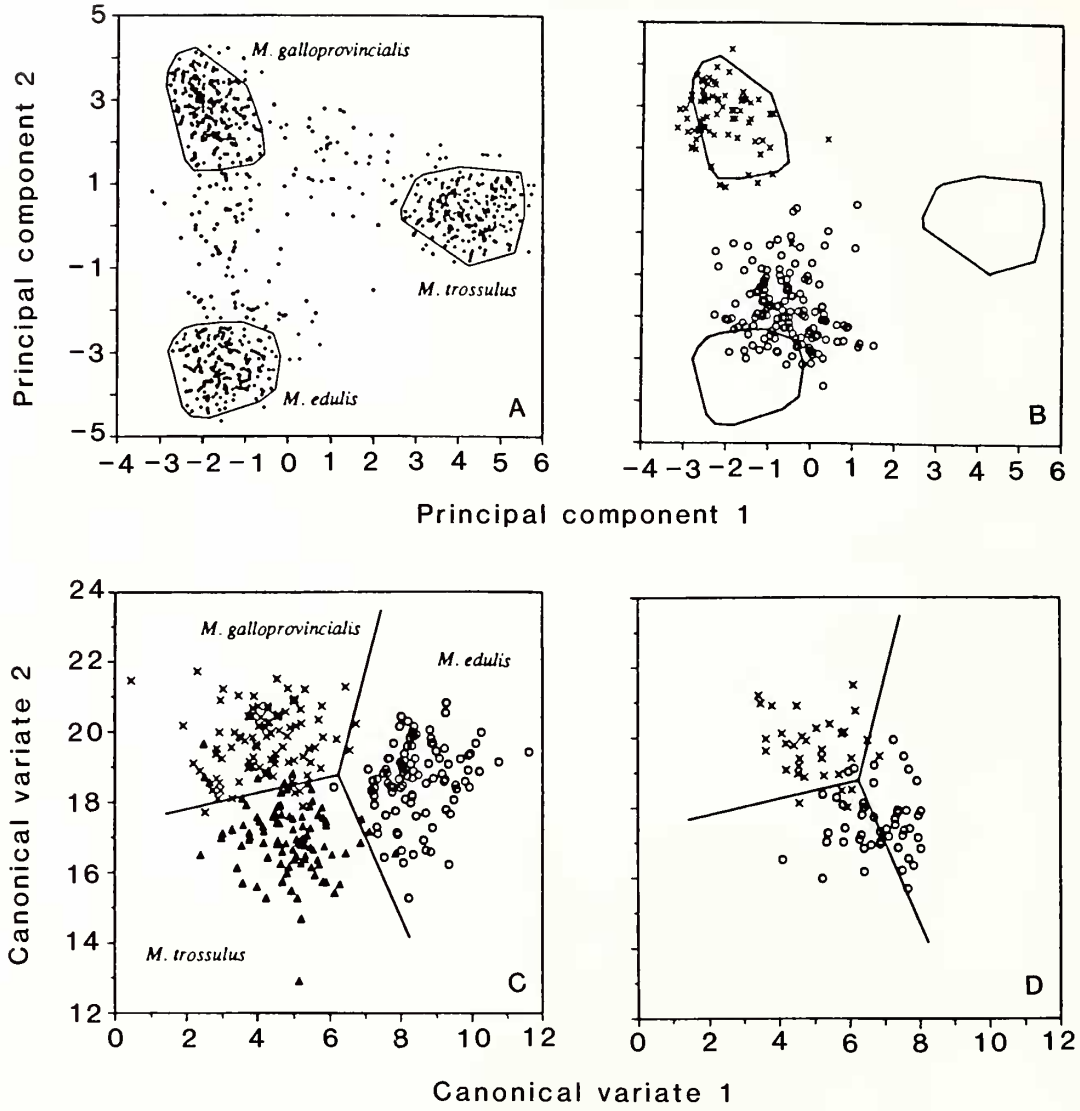

Fig. 1. First and second principal components of allozyme data for **A,** northern hemisphere, and **B,** southern hemisphere mussels. To aid visual comparison outlines have been drawn subjectively around the northern hemisphere clusters. **C, D,** First and second canonical variates of morphometric data for northern and southern hemisphere mussels respectively. Lines separating the northern hemisphere clusters have been drawn to aid comparison (after McDonald *et al.*, 1991).

3, 4).

In the mussel populations studied by Beaumont *et al.* (1989) the anterior adductor muscle to shell length ratios ([aams/sl]x10) in *Mytilus edulis* were consistently and significantly larger and the elongated scar more conspicuous than in its congener. The dark blue hinge plate in *M. edulis* is typically a more gently curved structure whereas in *M. galloprovincialis* it is usually paler in colour and describes a much tighter arc with the posterior end more closely delimited from the adjacent shell margin (Figs. 2B, C). Both the hinge plate to shell length ratio ([hp/sl]x10) and the length to width of the posterior byssal retractor scar (lbrs/wbrs) are significantly larger in *M. edulis*; in the latter ratio this is due almost entirely to variations in scar width rather than scar length. On virtually all of the morphometric criteria used by Beaumont *et al.* (1989), *M. galloprovincialis* at Rock were statistically indistinguishable from conspecifics from Polzeath and South Africa. Frequency distributions of several of these morphometric characters are illustrated in figure 5 and show that whilst the mean values between these two mussels are markedly different, there is, nevertheless, a considerable degree of overlap in the ranges of these individual shell characters.

The value of the anterior adductor muscle scar and hinge plate as taxonomic characters for separating *Mytilus edulis* and *M. galloprovincialis* has been reported by several workers. In most of these studies (e.g. Lewis and Seed, 1969; Seed, 1978; Wilkins *et al.*, 1983; Grant and Cherry, 1985;

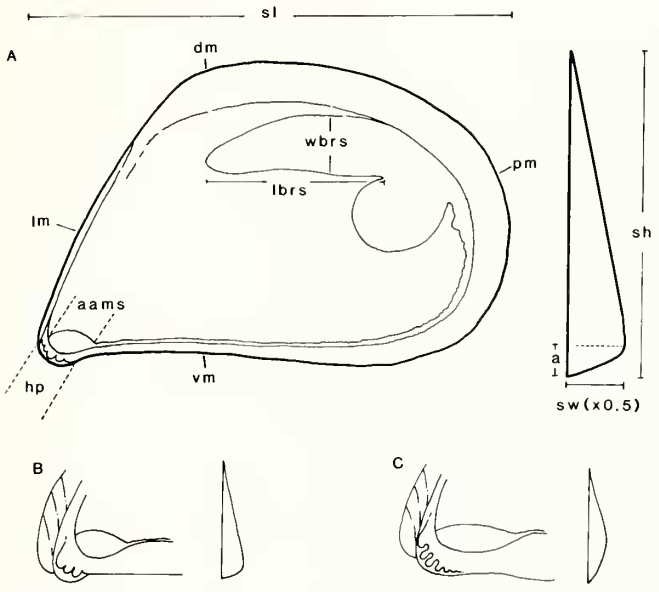

Fig. 2. A, Terminology of shell characters: a, position of maximum shell width along the dorso-ventral axis; aams, anterior adductor muscle scar; dm, dorsal margin; hp, hinge plate; lbrs, length of byssal retractor muscle sear; lm, ligamentary margin; pm, posterior margin; sh, shell height; sl, shell length; sw, shell width; vm, ventral margin; wbrs, width of byssal retractor muscle scar. Anterior end and transverse profiles of **B,** *Mytilus galloprovincialis* and **C,** *M. edulis* (after Beaumont *et al.*, 1989).

Lee and Morton, 1985) these characters have been considered separately but Verduin (1979) and Sanjuan *et al.* (1990) achieved a more effective separation when these were combined into a single taxonomic index. Other taxonomic characters previously used to separate these two mussels include the colour of the mantle edge, which is typically yellowish-brown in *M. edulis* and deep purple-violet in *M. galloprovincialis*, and the presence *(M. edulis)* or absence *(M. galloprovincialis)* of longitudinal rays of deeper colour in the shell (e.g. Hepper, 1957; Lewis and Seed, 1969).

By using four shell characters together with mantle edge colour and the genotypes of three enzyme loci (see p. 124) to identify *Mytilus edulis* and *M. galloprovincialis* Beaumont *et al.* (1989) were then able to test the reliability of each individual character against a final identification based on all eight characters. Table 2 shows the percentage of mussels that would have been misidentified using single taxonomic characters. The main point to emerge from this analysis was that no single character existed which allowed the certain identification of all mussels within these three populations. Overall, however, certain characters were clearly more reliable than others, though the diagnostic value of each character varied, sometimes quite markedly, both within and between sites. This applied equally to both morphometric and genetic characters. On average, single locus genotypes proved to be somewhat poorer diagnostic characters than the polygenic morphometric characters though significant differences between populations were more easily detected by the electrophoretic than by the morphometric data (Beaumont *et al.*, 1989).

It is clear from the above that *individual* morphological characters in *Mytilus* can vary, often on an exceedingly localised scale, and are therefore of limited taxonomic value though certain characters, or combinations of characters, do permit the separation of these two mussels with a high degree of confidence at least in certain populations. Multivariate techniques, on the other hand, have proved to be more successful in discriminating between mussels within the *M. edulis* species complex. Using a canonical variates analysis of 19 different morphometric characters in those samples from northern hemisphere locations where allozyme analysis had indicated previously the presence of a single species, McDonald *et al.* (1991) were able to resolve three distinct clusters corresponding to *M. edulis*, *M. galloprovincialis* and *M. trossulus* (Fig. 1C). Somewhat surprisingly, the best discrimination was between *M. edulis* and *M. galloprovincialis*, a long standing taxonomic problem in this genus. Canonical variates analysis finds the linear functions of the morphological variables with coefficients that maximize the distance between groups that have been previously identified using some other criteria, in this case allozyme characters. When the functions from the canonical variates analysis of northern mussels were applied to southern hemisphere samples, southern *M. edulis* was found to be morphologically intermediate between northern *M. edulis* and *M. trossulus*; southern and northern *M. galloprovincialis*, by contrast, were remarkably similar to each other (Fig. 1D). Characters wich have been considered previously useful for distinguishing *M. edulis* and *M. galloprovincialis*, such as the adductor muscle scar and hinge plate, also contributed most to the canonical variates analysis.

Thus, whilst some overlap occurred in the canonical variates, most individual mussels in these pure samples could be identified from shell characters alone when multivariate functions of all 19 morphometric variables were used. Individual characters, on the other hand, even those which are known to show the greatest variation between taxa, exhibited considerable overlap when these were considered singly. McDonald *et al.* (1991) also calculated canonical functions for each pair of northern mussels because all of the known areas of overlap between these mussels involve only two taxa. Results indicate that a linear combination of all characters in the canonical variate gives total separation in the case of *Mytilus edulis* and *M. galloprovincialis* (Fig. 6A) and an almost total separation of *M. edulis* and *M. trossulus* (Fig. 6B). For *M. galloprovincialis* and *M. trossulus*, which share several morphological traits, particularly with regard to their overall shell shape (Figs. 3, 4) and small size of the anterior adductor scars and hinge plates, there was a somewhat greater

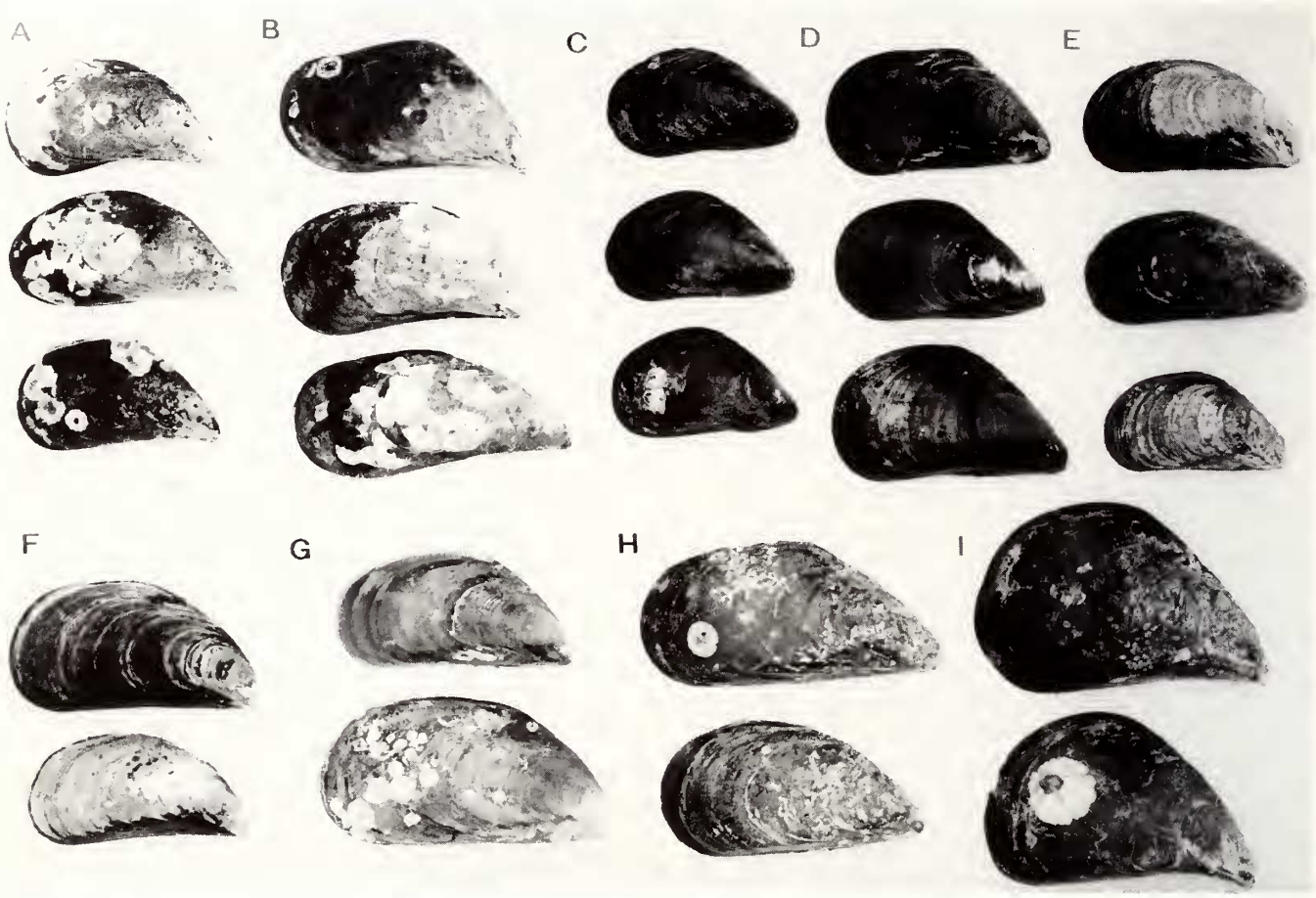

Fig. 3. *Mytilus trossulus* from: **A,** Tillamook, Oregon; **B,** Newport, Oregon. *M. edulis* from: **C,** Stony Brook, New York; **D,** Portland, Maine; **E,** Aarhus, Denmark; **F,** Falkland Islands; **G,** Mar del Plata, Argentina; **H,** Rock, S. W. England and *M. galloprovincialis* from: **I,** Rock, S. W. England (scale bar in cm).

degree of overlap (Fig. 6C). The posterior byssal retractor scar of *M. trossulus*, however, is characteristically much narrower than that of *M. galloprovincialis* of comparable shell length. Further research is now required to determine whether the morphometric differences described by McDonald *et al.* (1991) for pure mussel samples persist in areas of overlap and hybridisation. Moreover, by incorporating additional morphological characters into the multivariate analysis it would seem likely that an even better discrimination of these mussels could be achieved.

C) OTHER CRITERIA: Quite apart from the genetic and morphometric differences described above, *Mytilus edulis* and *M. galloprovincialis* are also known to vary in several other important respects. Figure 7 shows that, at Rock, spawning in *M. edulis* occurs mainly during May and June whereas *M. galloprovincialis* does not spawn until late July or August when seawater temperatures for this geographical locality are maximal. The cyclical pattern of reproduction is also less pronounced in *M. galloprovincialis* with significant proportions of fully ripe individuals persisting throughout much of the year. These differences are documented in detail elsewhere (Seed, 1971) but, in summary, extensive hybridisation at this particular site in south-west England seems most unlikely, a conclusion which is broadly supported by electrophoretic data (e.g. Skibinski *et al.*, 1983; Beaumont *et al.*, 1989). Temporal differences in spawning activity between these mussels have been reported similarly at another site in south-west England (Croyde) where *M. galloprovincialis* also had a greater estimated annual fecundity than *M. edulis* (Gardner and Skibinski, 1990); at a second site (Whitesand), however, there was a higher degree of genetic mixing resulting from reduced levels of variability in the timing of spawning and fecundity (Fig. 8).

Hybridisation can be induced artificially in the laboratory and when *Mytilus edulis* and *M. galloprovincialis* are crossed they produce fertile hybrids which can then backcross to the parent form to produce viable offspring (Lubet *et al.*, 1984). There would appear to be little evidence, therefore, of any *absolute* reproductive barrier or genetic in-

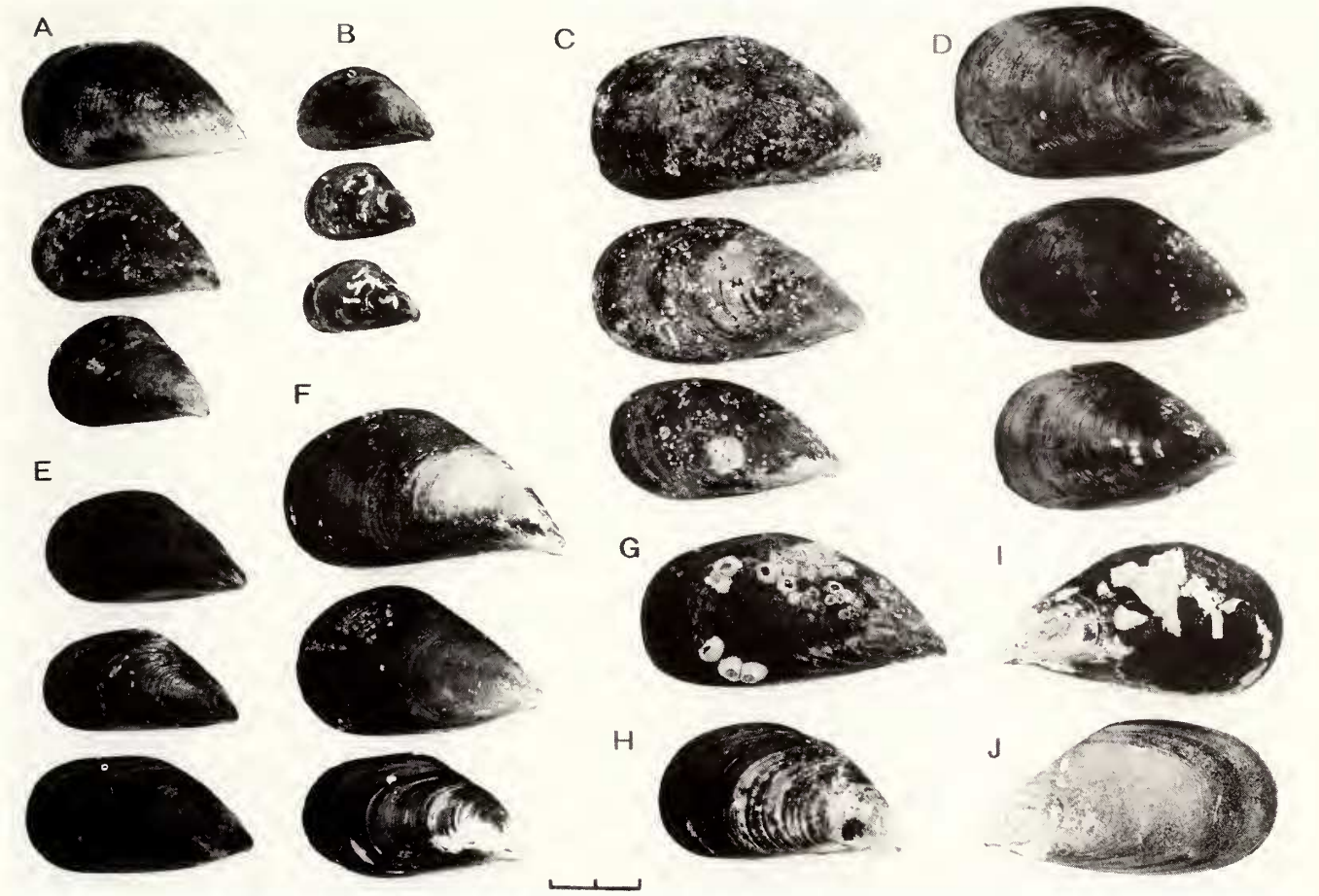

Fig. 4. *Mytilus galloprovincialis* from: **A,** Los Angeles, California; **B,** Victoria Harbour, Hong Kong; **C,** Albany, Western Australia; **D,** Huon River Estuary, Tasmania; **E,** Venice, Italy; **F,** West Cape coast, S. Africa; **G,** Newquay, S. W. England; **H,** Polzeath, S. W. England; **I,** Parede, Portugal; **J,** Vigo, Spain (scale bar in cm).

compatibility between these two mussels. However, whilst Lubet *et al.* (1984) apparently were unable to detect any adverse effects on viability, growth or mortality amongst the F^1 hybrids, recent research has shown that the mortality rates of hybrid larvae can be substantially higher than those of pure *M. edulis* or pure *M. galloprovincialis* larvae (Table 3).

Mytilus edulis and *M. galloprovincialis* can exhibit markedly different levels of infection by certain parasitic organisms (e.g. Seed, 1969, 1978; Coustau *et al.*, 1990; Hillman, 1990). Such differences appear to have a genetic rather than an ecological basis, and because these parasites can influence fitness through their effects on fecundity and condition, they could provide a potentially important selective force in sympatric mussel populations. Table 4 shows that on average approximately 30% of the *M. edulis* population at Rock is infested by the peacrab *Pinnotheres pisum* Penn. whereas in *M. galloprovincialis* the level of infestation is less than 2%. Several immunological (e.g. Bisignano *et al.*, 1980; Brock, 1985), histopathological (e.g. Hillman, 1990) and chromosomal (e.g. Thiriot-Quiévreux, 1984; Dixon and Flavel, 1986; Pasantes *et al.*, 1990) investigations are available for *Mytilus,* albeit with somewhat equivocal results. Significant differences in sperm size and morphology also have been described (e.g. Drozdov and Reunov, 1986; Hodgson and Bernard, 1986; Crespo *et al.*, 1990). Whilst the cytological differences reported within this genus are clearly insufficient to prevent hybridisation, they could, nonetheless, be partially responsible for maintaining species separation and could also presumably serve as useful taxonomic characters.

Only recently has the analysis of mitochondrial DNA variation been used in taxonomic studies of marine mussels (e.g. Skibinski, 1985; Blot *et al.*, 1990). Several pure and mixed populations of *Mytilus edulis* and *M. galloprovincialis* have been studied (e.g. Edwards and Skibinski, 1987; Fisher and Skibinski, 1990) and, whilst significantly different mtDNA genotypes were reported, none was perfectly diagnostic. There is little evidence, therefore, to suggest that

Table 2. Percentage of mussels which would have been misidentified using single taxonomic characters (from Beaumont *et al.*, 1989).

	n	Overall shape	aams[1]	hp[2]	Mantle colour	Raying	*Mpi*	*Est-D*	*Odh*
i) Rock:									
Mytilus edulis	64	0	0	4.7	0	17.2	23.8	3.2	25.0
M. galloprovincialis	76	34.2	17.1	10.5	6.6	1.3	7.9	9.4	36.5
ii) S. Africa:									
M. galloprovincialis	38	23.7	5.3	10.5	0	0	21.1	28.9	21.1
iii) Polzeath:									
M. edulis	3	0	0	0	0	33.3	66.6	0	33.3
M. galloprovincialis	81	11.3	19.4	9.7	0	3.2	48.4	88.7	32.3
Mean		16.8	11.8	8.8	1.9	6.1	26.7	35.1	29.8

[1,2] Anterior adductor muscle scar and hinge plate, respectively.

mtDNA variation provides any greater overall diagnostic power than allozyme variation in distinguishing between the different forms of *Mytilus* though mtDNA studies should ultimately lead to an improved understanding of both the population biology and taxonomy of this genus (Edwards and Skibinski, 1987).

ORIGINS AND DISTRIBUTION

With a geological record extending back for less than two million years, the genus *Mytilus* is of relatively recent origin (Seed, 1976). Amongst the smooth-shelled taxa, *M. edulis* generally is considered to be the ancestral species apparently having evolved from some more primitive infaunal or semi-infaunal modiolid stock (Stanley, 1972; Seed, 1990). *M. edulis* is widely distributed throughout the temperate latitudes of both hemispheres. In the northern hemisphere it occurs along the eastern seaboard of North America as far south as Cape Hatteras in North Carolina, but evidence now suggests that this species is absent from the Pacific coast of the north American continent (McDonald and Koehn, 1988). In Europe it extends from the Arctic waters of the White Sea and northern Norway southwards to north Africa (Seed, 1976; Suchanek, 1985) although recent work by Sanjuan *et al.* (1990) suggests that mussels along the whole of the Iberian peninsula could in fact be *M. galloprovincialis*, and that the

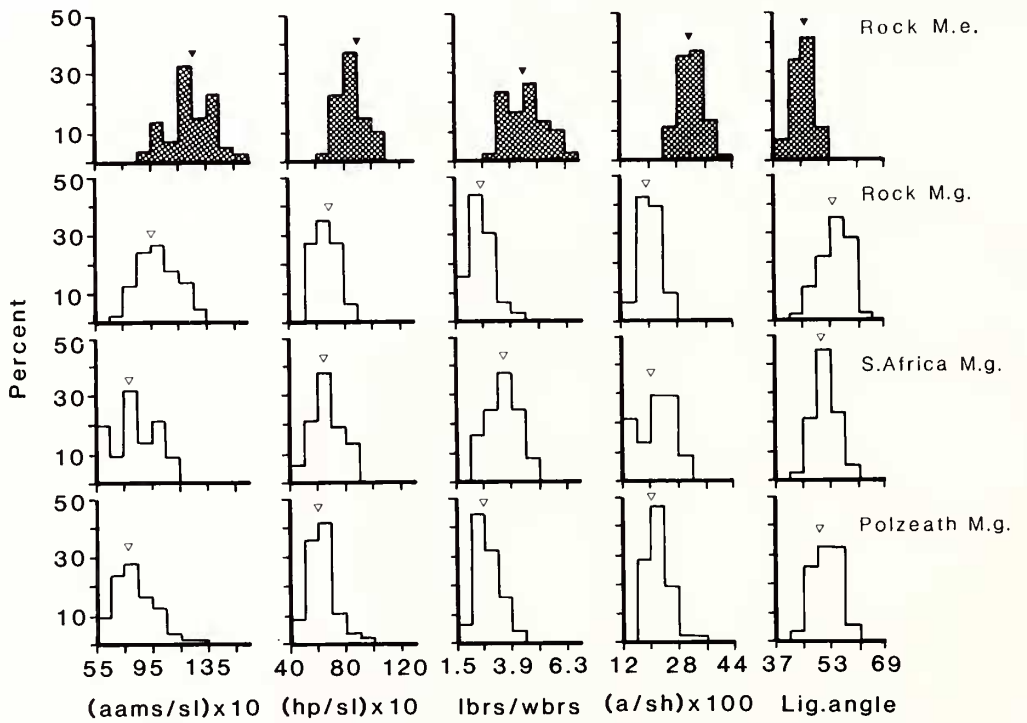

Fig. 5. Frequency distributions of several morphometric characters in *Mytilus edulis* and *M. galloprovincialis*. Mean values denoted by arrowheads. Note the similarity between the three *M. galloprovincialis* samples and how these differ from *M. edulis* (for abbreviations see figure 2) (after Beaumont *et al.*, 1989).

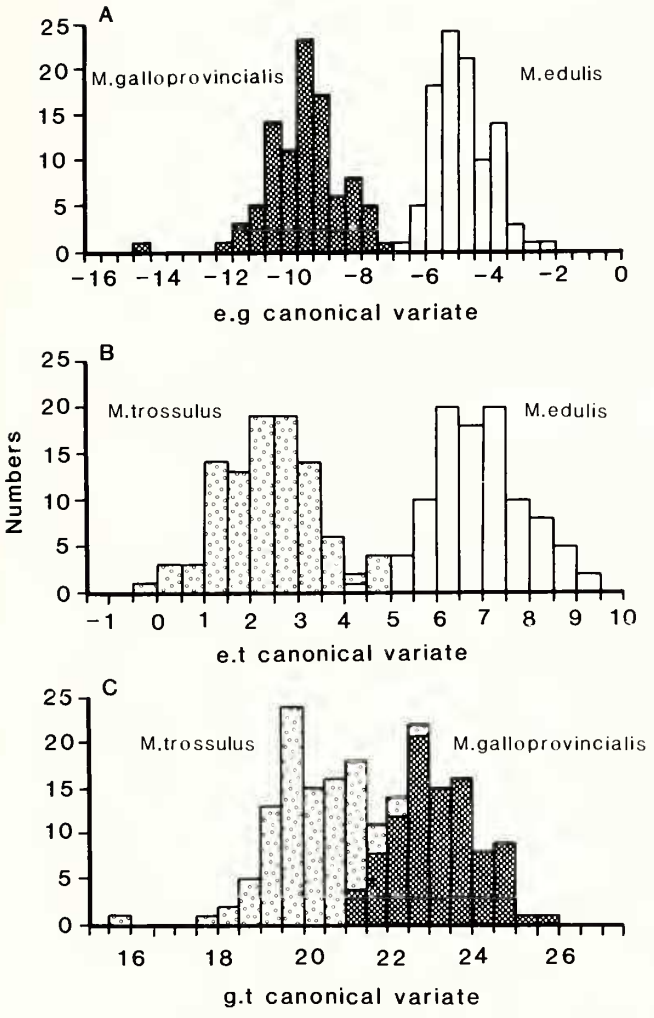

Fig. 6. Distribution of canonical variates for pairs of species from the northern hemisphere (after McDonald *et al.*, 1991).

southern limit of *M. edulis* is probably further north than was suspected previously. It is present in Iceland (Varvio *et al.*, 1988) and in Hudson Bay (Koehn, 1991), but its occurrence in Greenland, Novaya Zemlya and along the Arctic coast of Canada is still in question. In the southern hemisphere *M. edulis* occurs in the Falkland islands and along the east and west coasts of South America (as *M. platensis* and *M. chilensis* respectively). Mussels from the Kerguelen islands (= *M. desolationis*) are tentatively regarded as *M. edulis* (McDonald *et al.*, 1991).

Mytilus galloprovincialis also occurs in temperate waters of both hemispheres but its range extends into much warmer latitudes than *M. edulis*. This mussel is thought to have evolved from the *M. edulis* stocks which were present originally both on the Atlantic and Mediterranean coasts (Barsotti and Meluzzi, 1968). The warmer conditions which developed in the Mediterranean and the reduced contact between the Mediterranean and Atlantic during one of the Pleistocene ice ages favoured the differentiation of these stocks - a process which is probably still in progress (Seed, 1978). Recent studies on mtDNA suggest a divergence time between *M. edulis* and *M. galloprovincialis* which is consistent with palaeontological evidence (Fisher and Skibinski, 1990). Northerly migration of *M. galloprovincialis* probably occurred as the ice cap retreated, and in Europe this mussel is now present along much of the Atlantic coasts of Britain, France and Ireland where it coexists and hybridises to varying degrees with *M. edulis* (e.g. Seed, 1978; Gosling and Wilkins, 1981; Skibinski *et al.*, 1983).

M. galloprovincialis has also been introduced to areas far removed from its region of origin and in each case the introduced population is strikingly similar, both genetically and morphologically, to Mediterranean populations of this mussel. In the northern hemisphere its presence has been confirmed in California (McDonald and Koehn, 1988), Japan (Wilkins *et al.*, 1983), Hong Kong (Lee and Morton, 1985) and along the east China coast northwards as far as the border between Korea and the Soviet Union (McDonald *et al.*, 1991). These introductions were probably relatively recent events though *M. galloprovincialis* could have been present in California (as *M. diegensis*) since the turn of the century (McDonald and Koehn, 1988). In the southern hemisphere it occurs in South Africa (Grant and Cherry, 1985) and is widely distributed (as *M. planulatus*) throughout Australasia (McDonald *et al.*, 1991); its absence from South America is intriguing given the long history of trading between this Continent and countries bordering the Mediterranean.

Different allele frequencies between southern and northern populations of *Mytilus* have led to speculation that many southern mussel populations (of both *M. edulis* and *M. galloprovincialis*) could be native rather than introduced. Support for this view is provided by the occurrence of *Mytilus*-like fossils or subfossils in Australasia (Fleming, 1959; Don-

Table 3. Summary of laboratory fertilisation and larval survival experiments (Beaumont, Matin and Seed, unpub.).

Treatment[1]	Survival (%) after 3 days[2]	9 days[3]	Abnormal larvae (%)
pure lines:			
e/e; g/g	69	70	44
	ns	**	ns
hybrids:			
e/e; g/e	62	37	38

[1]Each treatment consisted of 12 replicates.
[2]All replicates started with 50 or 100 x 10^3 eggs.
[3]Cultures maintained at constant larval densities (numbers.ml^{-1}) by adjusting volume.
**$p < 0.01$; ns, not significant

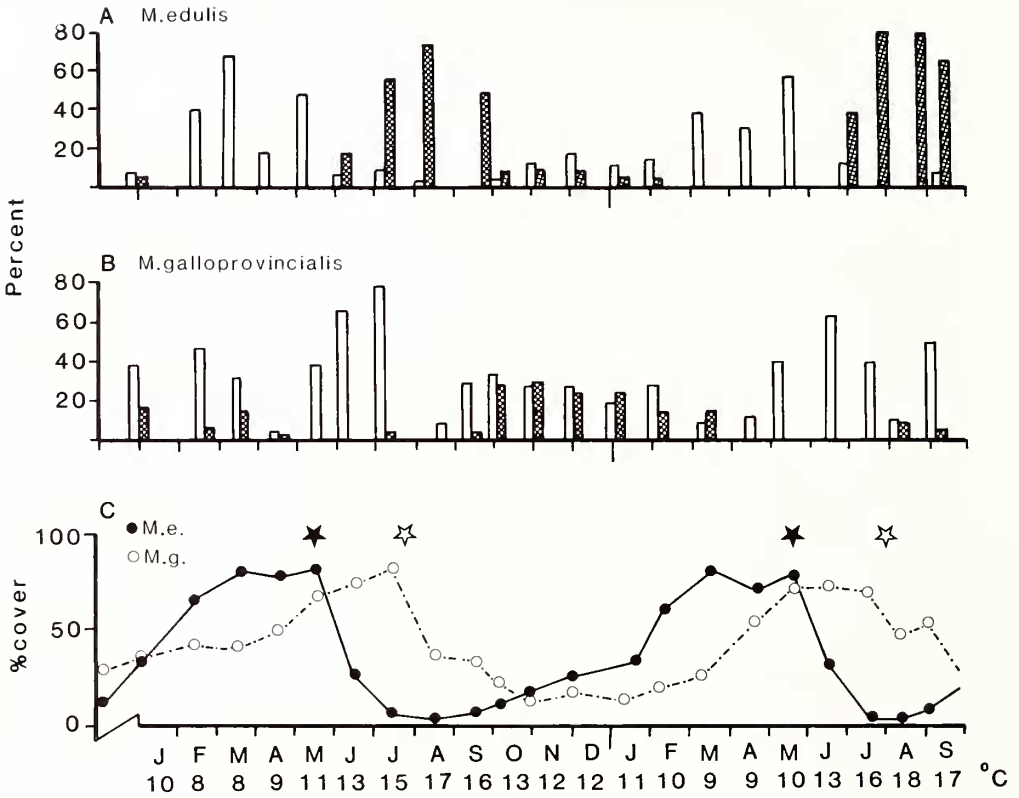

Fig. 7. Reproductive cycles of **A)** *Mytilus edulis* and **B)** *M. galloprovincialis* at Rock, S. W. England. Open columns denote ripe individuals, stippled columns spent individuals **C)** Area occupied by reproductive follicles in histological sections of mantle tissue; asterisks indicate onset of the main spawning periods (after Seed, 1971).

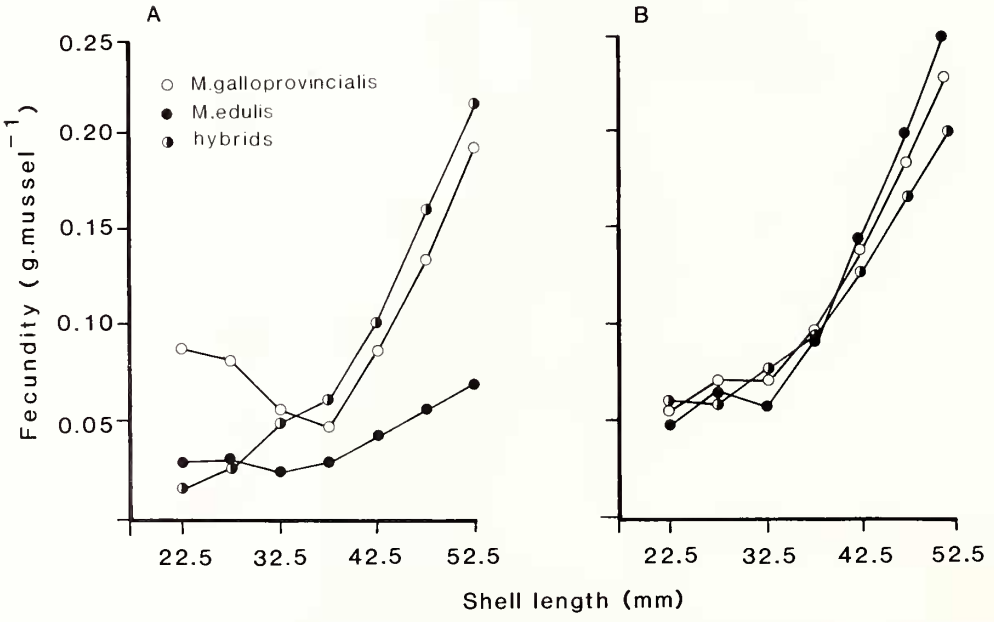

Fig. 8. Total annual fecundity as a function of genotype and shell length in mussels from **A)** Croyde and **B)** Whitsand, S. W. England (after Gardner and Skibinski, 1990).

Table 4. Incidence of *Pinnotheres pisum* and the proportions of *Mytilus edulis* and *M. galloprovincialis* in low shore mussels at Rock[1].

Date	*M. edulis* % infected (n)	*M. galloprovincialis* % infected (n)	Proportion (%) M.e.	M.g.
1. 1952[2]	—	—	15	85
2. Nov 1966; Jan 1968	30.5 (128)	4.5 (112)	—	—
3. Jun 1968	45.3 (316)	2.8 (212)	16	84
4. May 1968-Aug 1969	30.1 (718)	1.4 (768)	—	—
5. Oct 1985[3]	22.6 (230)	0 (148)	14	86
6. Oct 1989	—	—	17	83
Mean (total)	32.3 (1392)	1.8 (1240)	15.5	84.5

[1]All mussels exceeded the min. length (3.35cm) at which infection occurs.
[2]From Hepper (1957).
[3]Larger more heavily infected mussels less abundant than in earlier collections.

ner and Jungner, 1981; Kerrison and Binns, 1984) and South America (Johnson, 1976). The possibility still remains, however, that native species of *Mytilus* could have interbred subsequently with, or been largely displaced by, introduced mussels of northern origin. The absence of *Mytilus* from aboriginal shell middens and raised-beach deposits in South Africa and from early museum collections in Japan and South Africa (Wilkins *et al.*, 1983; Grant and Cherry, 1985) is consistent with the view that the present populations of *M. galloprovincialis* were introduced. Because *M. galloprovincialis* is widespread in the South Pacific, introductions into the northern Pacific need not, however, have originated in Europe (Koehn, 1991) though the genetic similarity between what are believed to be introduced populations and Mediterranean *M. galloprovincialis* would tend to argue against this view.

Mytilus trossulus has a rather disjunct distribution occurring in the colder waters along both sides of the Atlantic and Pacific oceans. It is present on the west coast of North America from central California to Alaska (McDonald and Koehn, 1988), along the Pacific coast of the Soviet Union (McDonald *et al.*, 1991), in the Maritime Provinces of northeastern Canada (Koehn *et al.*, 1984) and in the Baltic Sea (Varvio *et al.*, 1988; Bulnheim and Gosling, 1988). Varvio *et al.* (1988) have suggested a relatively ancient (1-2myr) northern origin for this lineage which probably evolved from some cold tolerant genotype during the Pleistocene glacial period; this could explain why its present distribution is broadly confined to regions just south of areas that were previously ice covered. Koehn (1991) argues that *M. trossulus* could in fact be a zoogeographical remnant of what was once a far more widely distributed mussel. To date, *M. trossulus* has not been recorded in the southern hemisphere.

Mytilus californianus is restricted to the Pacific coast of North America where it ranges from the Aleutian islands in Alaska to northern Mexico (Seed, 1976). *M. coruscus* occurs in Japan, and on the Pacific coast of Asia in China, Korea and Siberia (Scarlato, 1981). The geographical ranges of these two mussels, therefore, overlap with those of *M. trossulus* and *M. galloprovincialis* though *M. californianus* and *M. coruscus* are fairly easily differentiated from these smooth-shelled mussels on shell characteristics alone.

The global distribution of *Mytilus*, based largely on the extensive survey by McDonald *et al.* (1991), is illustrated in figure 9. This survey, however, was not intended to include the small scale sampling which will clearly be required in order to establish the precise geographical and ecological ranges of the various taxa, as well as the extent of hybridisation. The small scale variations in distribution are well illustrated by reference to one of the sites studied by McDonald *et al.* (1991), Posjet Bay in the Soviet Union, where mussels from an intertidal beach contained only *M. trossulus* whilst mussels from a floating dock just a few meters away were all *M. galloprovincialis.* At sites in Britain and Ireland, where *M. edulis* and *M. galloprovincialis* coexist, *M. galloprovincialis* often predominates on wave exposed shores, particularly at higher tidal elevations, whereas protected bays and estuaries are more typically favoured by *M. edulis* (e.g. Gosling and Wilkins, 1977, 1981; Skibinski *et al.*, 1983; Skibinski and Roderick, 1991; Gosling and McGrath, 1990). *M. galloprovicialis* is known to have stronger byssal attachment than *M. edulis* (Gardner and Skibinski, 1990, 1991) and also possesses shell features that enhance physical stability on hard surfaces (Seed, 1978, 1990). Such attributes could explain the apparent success of this mussel in high energy environments. It is interesting to note, therefore, that *M. californianus*, which shares several features with *M. galloprovincialis* (e.g. shell shape, strong byssal attachment) also predominates on wave exposed shores (Harger, 1972; Seed and Suchanek, 1992).

TAXONOMIC RELATIONSHIPS

Mytilus taxonomy has relied traditionally on morphological shell characters but these are greatly influenced by environment, and their diagnostic value is therefore often questionable. Enzyme electrophoresis, restriction analysis of

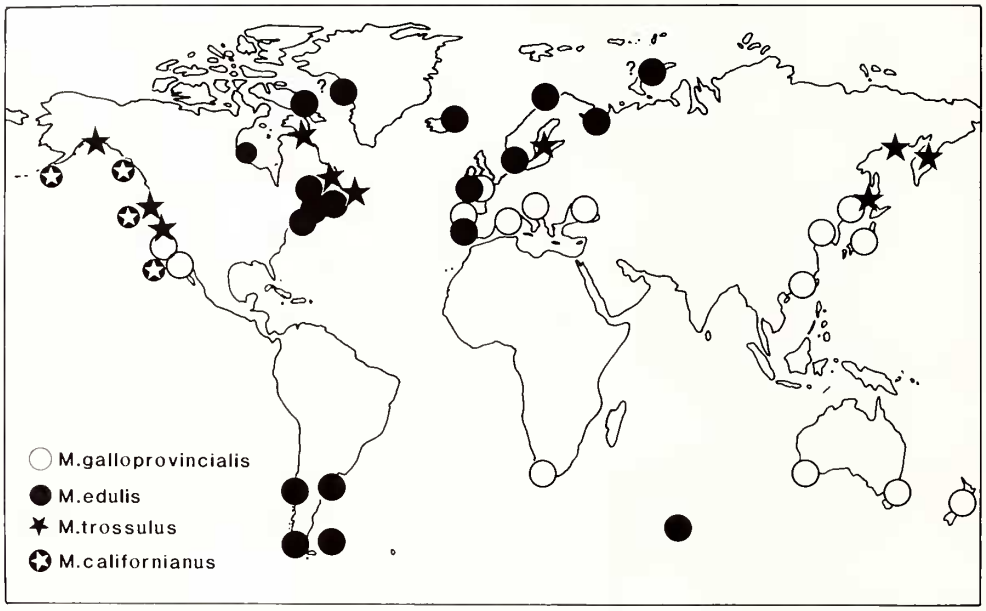

Fig. 9. Global distribution of the three smooth-shelled mussels, *Mytilus edulis, M. galloprovincialis* and *M. trossulus* (mainly from McDonald *et al.*, 1991). The distribution of *M. californianus* is also shown.

mtDNA and amino-acid sequencing are relatively free of environmentally induced changes and these techniques, together with immunological and cytological studies are now playing an increasingly important role in the systematic characterisation of *Mytilus* worldwide. At present, no single character exists which separates the three smooth-shelled taxa, *M. edulis, M. galloprovincialis* and *M. trossulus* unequivocally, though certain characters and combinations of characters are clearly more diagnostic than others. Recently, McDonald *et al.* (1991) effectively discriminated among these taxa using a multivariate approach and in all cases analyses of allozyme and morphometric data gave concordant results. Furthermore, mtDNA sequence variation data are so far broadly consistent with the taxonomic judgements based on both allozyme and morphometric data (Koehn, 1991). Such studies serve to emphasise the value of a multidisciplinary approach in resolving complex taxonomic problems.

Whether *Mytilus edulis, M. galloprovincialis* and *M. trossulus* should be considered as separate species has been the focus of considerable discussion (e.g. Gosling, 1984; Skibinski *et al.*, 1983; Blot *et al.*, 1988; Bulnheim and Gosling, 1988; Johannesson *et al.* 1990; Väinölä, 1990). One reason for the reluctance to consider these taxa as distinct species is that in areas of geographical overlap allozyme characters indicate varying degrees of hybridisation and introgression (e.g. Skibinski and Beardmore, 1979; Gosling and Wilkins, 1981; Skibinski *et al.*, 1983; McDonald and Koehn, 1988; Koehn, 1991; Väinölä and Hvilsom, 1991) with the concommitant mixing of morphological characters (e.g. Seed, 1972, 1974). Unfortunately, there is no generally accepted maximum amount of hybridisation which two taxa can exhibit and still be considered separate species. Hybrid zones of these mussels vary in size and are spatially complex with pure, mixed and hybrid populations occurring in a patchwork pattern. The most geographically widespread hybridisation occurs between *M. edulis* and *M. galloprovincialis* existing from the Biscay coast of France or even northern Spain to parts of northern Britain. Hybridisation between North Sea *M. edulis* and Baltic *M. trossulus*, by contrast, occurs over a relatively narrow zone in the Danish Belt Sea. Contact between *M. edulis* and *M. trossulus* in North America is poorly documented, but from the available evidence hybridisation occurs at several sites in the upper reaches of the Gulf of St. Lawrence. In central California *M. galloprovincialis, M. trossulus* and their hybrids are present. No hybridisation has so far been reported in the region near the border between Korea and the Soviet Union where there is contact between *M. trossulus* and *M. galloprovincialis*, but this could simply reflect the lack of detailed information for this particular geograpical area.

Hybrid zones between these mussels also appear to be relatively stable indicating that although gene flow does occur, the parent forms can still maintain their genetic (and morphological) integrity. In south-west England the proportions of *Mytilus edulis* and *M. galloprovincialis* have remained virtually unchanged over a period of almost 40 years (Table 4) despite the occurrence of hybridisation. Moreover, these proportions are virtually identical amongst all size categories of mussels (but see Gardner and Skibinski, 1990). We have no clear evidence therefore that *M. galloprovincialis* in this

particular geographical locality is gradually replacing *M. edulis*; this is perhaps surprising in view of the higher fecundity and competitive edge that *M. galloprovincialis* apparently enjoys over its congener (e.g. Gardner and Skibinski, 1988, 1990, 1991; Skibinski and Roderick, 1991). If directional selection in favour of *M. galloprovincialis* is occurring then it is obviously being offset by the immigration of *M. edulis* from other localities. Current genetic and morphometric data suggest that gene flow between *M. edulis* and *M. galloprovincialis* in the Rock population is limited. This of course partly reflects the different reproductive cycles of these two mussels at this site (Fig. 7) although in laboratory experiments we now know that hybrid larvae can experience heavy mortality rates (Table 3) thus presumably contributing to the temporal genetic stability in sympatric populations of these two mussels (see also Gardner and Skibinski, 1988; Gosling and McGrath, 1990). A considerable amount of selection against hybrid individuals could therefore conceivably occur *before* juvenile mussels are actually recruited to the established population.

Despite the lack of any absolute reproductive barrier and the massive potential for dispersal via a planktonic larval stage that can last for several weeks, populations of *Mytilus edulis, M. galloprovincialis* and *M. trossulus* comprise relatively homogenous groups each maintaining a unique genetic and morphological phenotype across vast distances. This distinctiveness warrants recognition and it is perhaps appropriate therefore to consider these taxa as three distinct species despite the occurrence of localised hybridisation (McDonald *et al.*, 1991). Differences in mtDNA fragments, sperm size and structure, as well as chromosomal variations (p. 129) further support the taxonomic interpretation that the genetic differences between these mussels are quite substantial and that they ought therefore to be accorded separate and equal systematic status. In an earlier paper (Seed, 1978) I have argued that *M. galloprovincialis* could be an emerging species, reaching specific status in certain parts of its geographical range whilst freely interbreeding elsewhere. Far from straining the biological species concept this merely emphasises the problems inherent in extending the concept geographically. Tentative synonomies of *Mytilus* are summarised in Table 5.

It is clear from the *Mytilus galloprovincialis* controversy that a multidisciplinary approach is required if the complex systematics of the genus *Mytilus* are to be satisfactorily resolved. In addition to further research using allozyme and morphometric characters, particularly applied to the hitherto poorly studied populations in the southern hemisphere, promising areas for future work include: 1) studies of reproductive cycles and fecundity in sympatric populations; 2) measurements of survival, growth and physiological parameters in natural and laboratory hybrids; 3) studies of abnormal development, growth and survival in pure and hybrid larvae; 4) reciprocal transplants of mussels between the ranges of the different taxa; 5) comparisons of sperm morphology and an extension of the mtDNA, karyological and immunological studies of mussels from pure and hybrid populations. The aim of this research should not be to determine once and for all whether these *Mytilus* taxa are 'good species'. This is unresolvable without an agreed operational definition of a biological species and in any case is perhaps a somewhat semantic question largely devoid of biological interest. Instead, future research should concentrate on the biological processes which keep these taxa distinct despite the widespread occurrence of hybridisation.

Table 5. Simplified and tentative synonymies of *Mytilus* spp.

i) *M. edulis* Linnaeus	(=*M. platensis* Orbigny *M. chilensis* Hupé *M. desolationis* Lamy = *M. kerguelensis* Fletcher)
ii) *M. galloprovincialis* Lamarck	(=*M. diegensis* Coe *M. planulatus* Lamarck *M. aoteanus* Powell *M. zhirmunskii* Scarlato and Starabogatov)
iii) *M. trossulus* Gould	(=*M. kussakini* Scarlato and Starabogatov)
iv) *M. californianus* Conrad	
v) *M. coruscus* Gould	[=*M. crassitesta* Lischke (=*M. californianus?*)]

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